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Discoid gemmae in the leafy hepatics of New England

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The gemmae found among the leafy Jungermanniales belong, with very few exceptions, to two distinct types. Those of the simpler type are unicellular or bicellular bodies which arise, generally in clusters, from the leaves or from the stem in the region of the apex. Those of the second type are discoid, multicellular bodies which are borne either on the margins or the surfaces of the leaves. The formation of the simpler type of gemma seems often to be associated with limitation of growth, for when the gemmae are borne on the stem the entire growing point goes over to the production of gemmae. The production of discoid gemmae, however, rarely seems to affect the growth of the plant to any marked degree. Gemmae of the simple type are of much more frequent occurrence, especially among northern forms, and are found in the vast majority of the gemmiparous New England species. Discoid gemmae occur, on the other hand, chiefly among the tropical epiphyllous forms. In New England they are known in only two species, *Cololejeunea Biddlecomiae* (Aust.) Evans and *Radula complanata* (L.) Dumort. According to Nees von Esenbeck discoid gemmae occur also on *Lejeunea cavifolia* (Ehrh.) Lindb. (*L. serpyllifolia* Lib.), but as he describes them, they represent here actual pieces of the leaf which become separated and are therefore hardly to be considered differentiated gemmae.

In the present paper the development and structure of the gemmae of *Cololejeunea Biddlecomiae* and *Radula complanata* are discussed. Both of these species are widely distributed in North America, and *Radula complanata* occurs also in Europe, Asia, and northern Africa. The material used in the study of *Cololejeunea Biddlecomiae* was collected by the writer in Woodbridge, Connecticut, in March. Material from Superior, Wisconsin, collected in August by G. H. Conklin, was used for comparison. The material of *Radula complanata* was collected in North Haven, Conn., in October, specimens collected at Woodbridge, Conn., in March, and at Lentz, Switzerland in September, being used for comparison. All the *Radula* material used was collected by Professor A. W. Evans.

But little has been written concerning the gemmae of the leafy Jungermanniales. In the tropical genus *Cyclolejeunea*, however, the gemmae have been described by Evans in four species. In *Cololejeunea* the development and structure of the gemmae have been described by Goebel in the Javan *C. Goebelii* (Gottsche) Schiffn. and by Cavers in the European *C. calcarea* (Lib.) Schiffn. For *Radula* the development of the gemmae has also been briefly treated by Goebel in two Javan species, *R. Hedingeri* Goeb. and *R. tjibodensis* Goeb., and by Cavers in *R. complanata*.

COLOLEJEUNEA BIDDLECOMIAE.

The gemmae in *Cololejeunea Biddlecomiae* are borne on the surface of the leaves, most frequently on the lower surface of the lobes, occasionally on the upper surface and never, at least in the material examined, on the lobules. Usually only a few, not more than five or six, are borne on a single leaf. Gemmae appear to be of rather general occurrence in this species, though only a comparatively small proportion of the plants in any individual mat are gemmiparous and plants bearing a considerable number of gemmae are found closely associated with plants having none. Gemmae are found more abundantly on sterile plants, but the presence of sexual organs by no means prevents the formation of gemmae. In fact they are found occasionally on the bracts, but never, so far as could be determined, on the perianths.

In the formation of a gemma a leaf cell first projects beyond the surface of the leaf and the projecting portion is cut off by a wall parallel to the leaf surface. The outer cell, which is nearly circular in outline, becomes the mother-cell of the gemma, while the inner one may be regarded as a stalk. The gemma mother-cell then undergoes a series of regular divisions by walls perpendicular to the surface of the leaf. The first wall divides it into two approximately equal parts (FIG. 1, A) and each of the semicircular cells then divides by a wall perpendicular to the first, so that the gemma in the four-celled stage consists at first of approximately equal quadrants (FIG. 1, B).

One of these quadrants in each half usually grows more rapidly than its sister cell and thus displaces the wall separating them, so that each half of the gemma soon consists of two unequal cells symmetrically placed with respect to the median wall (FIG. 1, C). Each of the larger cells then begins to function as a two-sided apical cell (FIG. 1, D and E) and cuts off three segments, the first by a wall approximately parallel to the median wall. Each segment in turn divides by a periclinal wall and the outer cell of the first segment divides further by an anticlinal wall. Each of the smaller, or basal, cells also divides regularly. The cell divisions normally take place exactly as they do in the first apical segment, so that each basal portion of the mature gemma contains three cells (FIG. 1, D and E). Occasionally, however, one of the outer cells divides again by a periclinal wall (FIG. 1, F).

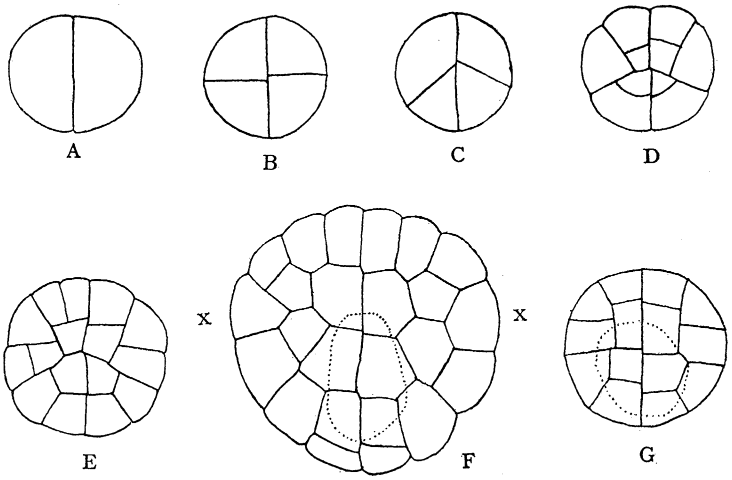

FIGURE 1. A–F. *Cololejeunea Biddlecomiae.* A–E. Gemmae in various stages of development, × 600. F. A gemma about ready to separate (x, apical cell), × 600. G. *Cololejeunea calcarea.* A gemma in which the basal and apical quadrants are nearly equal, × 600.

The gemmae increase in size somewhat, after cell division has ceased, by the growth of the cells themselves; and this growth continues, for a time, after the gemmae are shed. This is clearly shown by the fact that the gemma, at the time it is shed, is about 0.035 mm. in diameter, while it is common to find gemmae loose in the material containing precisely the same number of cells, yet having a diameter of 0.055 mm. or more. The cells of the gemma meanwhile increase proportionately in size, that is, from about 7 μ to about 12 μ in average diameter or to slightly less than the average diameter of the cells of the lobe.

A mature gemma is typically a flat disc consisting of a single layer of cells and showing no indication of dorsi-ventral differentiation. It is composed of symmetrical halves, each consisting of eleven or twelve cells. In each half eight of these cells come from the apical cell and its three segments and three or four come from the basal cell (FIG. 1, F). The gemma is regular in outline, without marginal hairs or other projecting cells, and there is no indication of rhizoids or other organs of attachment such as described by Goebel in the epiphyllous *C. Goebelii*. The one-celled stalk is attached to the gemma along the median line in the basal region (FIG. 1, F and G). The separation of the gemma takes place as in other *Lejeuneae* by the splitting of the cell wall between the stalk cell and the gemma.

The above description agrees closely with Goebel's account (50, *f. 55*) of the development of the gemma in *Cololejeunea Goebelii*, except that he describes the first anticlinal wall as dividing the semicircular cell into unequal portions. This condition in *C. Biddlecomiae*, at least, seems to be secondary, due to the more rapid growth of the cells which are to function as apical cells. This appears from the fact that the condition of equal quadrants (FIG. 1, B) is of frequent occurrence in the four-celled stages observed.

The development of the gemmae in *Cololejeunea Biddlecomiae*, as traced by the writer, differs in several respects from that figured by Cavers (160, *f. 8*) in the closely related *C. calcarea*. Cavers figures the cell divisions as taking place by cell walls parallel to and at right angles to the median line, without reference to an apical cell, and implies that the mature gemmae differ from those of *C. Goebelii* in not having an apical cell. He states also that the stalk cell is inserted at the center of the gemma. In order to determine whether *C. calcarea* really differs from other members of the genus in these respects, material from Pottenstein in Upper Franconia, Germany, collected by Arnold (Hep. Europ. *283b*) was examined. This showed that the gemmae of the two species are essentially alike in their development, form, and method of attachment. One immature gemma of *C. calcarea*, however, was found in which the first anticlinal walls had not been displaced by the growth of the apical cells (FIG. 1, *G*). The basal and apical quadrants are thus nearly equal, and the gemma as a whole appears more like those figured by Cavers. It is very probable that it was from such a condition as this that his figures were taken.

RADULA COMPLANATA.

In *Radula complanata* the gemmae are borne on the edges of the leaves, frequently at right angles to the leaf surface. A single leaf often bears a considerable number of gemmae and it is common to find leaves where every cell for a considerable portion of the margin has given rise to a gemma. Gemmae are of more frequent occurrence in *R. complanata* than in most species. In fact so general is their occurrence that it is comparatively rare to find well-developed plants which do not bear gemmae. Moreover, it is evident that there can be here no such antagonism between the production of gemmae and of sexual organs as has been supposed by some writers, for the gemmae are frequently borne on the edge of the perianth itself, as well as on the bracts.

Each gemma arises from a single marginal cell, which projects beyond the cells on either side and becomes at once the mother-cell of the gemma. This cell as it increases in size secretes a gelatinous substance which may be noted around the edge of the cell. The secretion of this gelatinous substance appears to be characteristic of rapidly growing cells in the gemma and the occurrence of gelatinous material in considerable quantity may be taken as a rough indication of the region of most rapid cell division (FIG. 2, *A*, *C*, and *D*; FIG. 3, *A*; and FIG. 4, *A* and *C*). The gemma mother-cell divides first by a periclinal wall (FIG. 2, *A*). This wall is sometimes perpendicular to the surface of the leaf, but is more often so inclined that the outer of the two cells, which is generally the larger, overlies a portion of the inner cell. The outer cell, which gives rise to the main portion of the gemma, divides first by a longitudinal wall (FIG. 2, *B*). The inner cell divides later by a longitudinal wall and forms the two-celled basal portion of the gemma, which may be regarded as a poorly defined stalk.

The two cells formed by the division of the outer cell behave as more or less independent portions. They divide without very definite order by transverse and longitudinal walls (FIG. 2, *C*) and soon a wedge-shaped cell is cut off in one (FIG. 2, *D*) or both (FIG. 2, *E*) of the portions. These cells function for a while as two-sided apical cells. The irregular occurrence and behavior of these apical cells gives rise to the considerable variation in form which is to be observed in the gemmae of *Radula complanata*. For both portions may cut off apical cells at the same time and develop with equal rapidity, thus forming a symmetrical gemma, or one segment only may form an apical cell, in which case the segment which has no apical cell will develop very little and will be more or less crowded out of position. Such a gemma is shown in FIG. 3, *A*. One portion has here developed an apical cell which has cut off six segments. This portion has increased by further cell divisions until it is composed of twenty-three cells, while the portion having no apical cell is composed of but four cells.

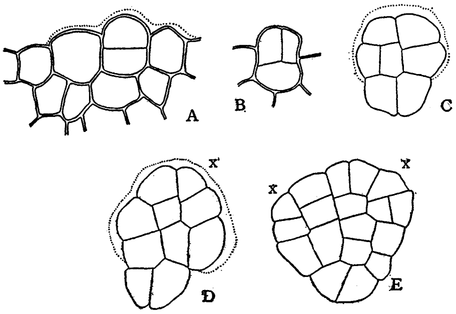

FIGURE 2. *Radula complanata*. *A–C*. Gemmae in early stages of development, × 300. *D*. Gemma that has formed one apical cell, × 300. *E*. Gemma with two apical cells, × 300. Dotted line indicates gelatinous secretion.

Moreover, the apical cells do not persist until the gemma is mature; but, after cutting off segments in regular succession for a time, lose their capacity of regular segmentation and divide by a periclinal wall (FIG. 3, *B* and *C*). After this first periclinal division the apical cell divides like other cells by longitudinal and transverse walls, but the segments which have arisen directly from the division of an apical cell may generally be traced by their position in the mature gemma. In gemmae having two apical cells one may continue to function as an apical cell after the other has lost its power of regular segmentation and has begun to divide by periclinal and anticlinal walls (FIG. 3, *D*). This gives rise to still greater irregularity in the mature gemmae. The usual position of the mature gemmae, at right angles to the plane of the leaf, seems to be due to the crowding of the gemmae as they increase in size. For the gemmae are at first in the plane of the leaf and remain so in places where they are not close together.

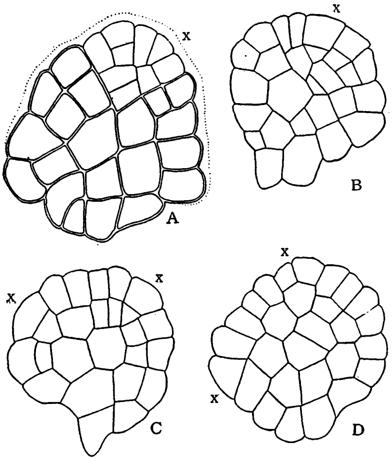

FIGURE 3. *Radula complanata*. *A*. Gemma with one apical cell. *B–D*. Gemmae in which the apical cells have ceased to cut off regular segments and have divided irregularly. × 300.

The active division of an apical cell tends to inhibit the division of other cells in the gemma. This appears from the fact that when one apical cell is present the portion lacking an apical cell exhibits very little cell division. It is shown still more strikingly, however, by the fact that about the time the apical cell loses its power of active segmentation the older cells of the gemma begin to divide by walls parallel to the surface.

A mature gemma, that is, one ready to fall from the leaf is thus typically two cells thick for a considerable part of its extent (FIG.

4, *A* and *B*). The marginal cells, however, rarely divide by walls parallel to the surface and the basal cells never take part in this division. In this respect *R. complanata* apparently differs markedly from other members of its group. For in all the other leafy Jungermanniales thus far observed, which bear thalloid gemmae, the gemmae are but one cell thick throughout (Evans, 298).

In the mode of separation of the gemmae, also, *Radula complanata* differs from many other leafy Jungermanniales. For while the separation is schizolytic, the splitting takes place in the wall between the basal cells and the cells of the leaf. The two-celled stalk is thus retained as a part of the mature gemma when it falls from the plant. This is very different from the condition found in *Cololejeunea*, where the separation takes place between the gemma and the stalk cell. A similar difference has been noted by Evans (277, 284, *f. 4, 9*) in the separation of the gemmae in *Metzgeria*. In *M. crassipilis*, for example, the gemmae are set free by a splitting of the wall between the gemma and the cell cut off by the original horizontal wall, while in *M. furcata* separation takes place by the basal cells splitting away from the adjacent thallus cells.

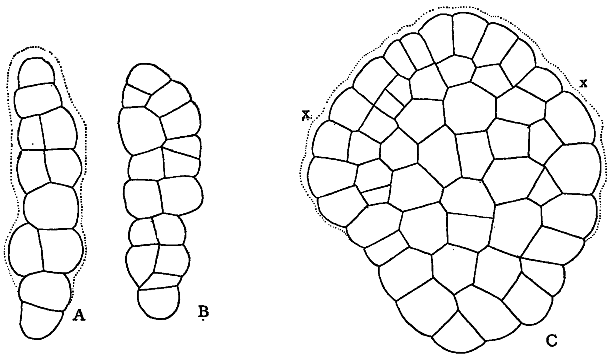

FIGURE 4. *Radula complanata*. *A* and *B*. Mature gemmae in optical rection. *C*. Surface view of mature gemma. × 300.

In no case was a mature gemma observed which still retained an apical cell. This is contrary to the statement of Cavers (159) that the mature gemma "shows on its distal margin a large apical cell, triangular in surface view."

The development of the gemmae in *Radula complanata* differs considerably from that of *R. Hedingeri* as described by Goebel (52). He states that the gemma mother-cell divides by a number of longitudinal walls between which transverse walls are formed and that no apical cell is developed in the gemma. That this is not the case in *R. complanata* is clear from the almost invariable occurrence of apical cells in the young stages observed, and from the fact that in mature gemmae the position of the apical cell may generally be traced. FIG. 4, *C*, shows what may be considered a typical gemma. In this the outlines of the two apical cells with their segments may be clearly traced though each of the apical cells has become divided into five cells.

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LITERATURE CITED

Cavers, F. On asexual reproduction and regeneration in Hepaticae. New Phytol. **2**: 121–133, 155–165. 1903.

Evans, A. W. Hepaticae of Puerto Rico—IV. *Odontolejeunea*, *Cyclolejeunea*, and *Prionolejeunea*. Bull. Torrey Club **31**: 183–226. *pl. 8–12.* 1904.

Evans, A. W. Vegetative reproduction in *Metzgeria*. Ann. Bot. **14**: 271–303. 1910.

Goebel, K. Ueber epiphytische Farne und Muscineen. Ann. Jard. Buitenzorg **7**: 1–73. *pl. 1–9.* 1887.

Nees von Esenbeck, C. G. Naturgeschichte der europäischen Lebermoose **3**: 274. Breslau, 1838.